Sensitivity Analysis of a Stage Structure Omnivory Model

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Abstract

The world of ecology is constantly changing and species survival often depends on approximations and measurements taken by biologists. These approximations help to ensure and predict the future of the given species. Our ecological community of interest involves a unique mixture of competition and predation known as omnivory - feeding on more then one trophic level. We then use a sensitivity analysis to determine how small changes in parameter values affect the solution to the system. Sensitivity analysis proves the importance in determining which parameters require the most attention from biologist to ensure the survival of that species. This mathematical evidence gives biologist crucial information about the future of these species and how each species reacts when small changes occur in parameter values. Our results showed that the mortality rate of the predator was the most sensitive parameter and the time the predator handles the consumer was the least sensitive of our parameter values.

Key Words: Stage-Structure, Omnivory Model, Sensitivity Analysis

1 Introduction

The long term survival of species should be of utmost importance to humans. Human survival depends on biodiversity and the understanding of natural systems. Most natural systems are very complex multispecies food webs which can be unmanageable for detailed analysis. Therefore, to gain some insight into the world around us, we must look at a smaller number of species and their interactions within their community. This can be used to get a better understanding of the interactions among more complex natural systems.

I would like to focus on the combination of competition and predation interactions within a community, also known as omnivory. However, I really want to focus on stage structure omnivory by concentrating on four species: the adult predator, the juvenile predator, the consumer, and the resource. This will allow us to use mathematical calculations to help us to see how each species depends on one another and will allow us to do a sensitivity analysis on our model.

2 Basic Concepts

2.1 Species Interatctions

In order to understand omnivory better, we must know a few basic species interactions. The first one is competition, which is pretty self explanatory. One species competes with another species for the same resource. For our particular model, the adult predator, the juvenile predator, and the consumer are all competing for the same resource.

The next species interaction we are going to look at is predation. This eliminates competition out of the model completely and is strictly one higher trophic level species preying on another lower trophic level species. (A trophic level is a step in a nutritive series or food chain of an ecosystem.) This means for our model that only the predator (adult and juvenile) eats the consumer, and the consumer only eats the resource.

2.2 Ominvory

Now that we understand the basic interactions among species, competition and predation, we can now define and start to analyze our stage structure omnivory model.

Definition 2.1. Omnivory is defined as the act of feeding on resources at different trophic levels.

Omnivory is the combination of species interactions, competition and predation. Competition and predation can be very complex and intricate, but for our purposes we will use the simplest form of omnivory. By simplest I mean the consumer and the juvenile predator feeds solely on the resource and the adult predator feeds on the resource and the consumer.

2.3 Existence and Uniqueness

We will use the following theorem from Walter to show local existence and uniqueness of solutions to our initial value problems, for all time, $t \geq 0$.

Theorem 2.2. *Let $\mathbf{f}(t, \mathbf{x})$ be continuous in a domain $D \subset {\mathbb{R}_+}^{n+1}$ and satisfy $\frac{\partial f}{\partial x}$ is continuous in D. If $(t_0, \mathbf{c}) \in D$, then the initial value problem*

$$\mathbf{x} = \mathbf{f}(t, \mathbf{x}), \quad \mathbf{x}(t_0) = \mathbf{c}$$

has exactly one solution. The solution can be extended to the left and right up to the boundary of D.

2.4 Sensitivity Analysis

Models are developed to approximate natural systems. This fact imposes a limitation on the confidence we place on the model's outcome. Since we are approximating the natural system, the inputs should be subject to certain variability. Our model parameters are limited by measurement error, as well. We will use sensitivity analysis to obtain this outcome.

Definition 2.3. Sensitivity analysis involves the use of analytical and/or computational tools to evaluate how changes in inputs affect model response variables.

The inputs may be initial conditions or model parameters. The model response variables may be population densities, state variables, population growth rates, consumption rates, handling rates, etc. There are unlimited variations and applications of sensitivity analysis.

One of the most important questions from our model is, how do small changes in model parameter values affect the population densities. This will help us to determine which parameter estimates are sufficiently precise for our model to give reliable predictions. We will also be able to prioritize the parameters to help biologists determine which parameter values should be most precisely and accurately estimated when they collect data.

3 Stage Structure Omnivory Model

Having some intuition of what omnivory consists of, we now introduce a standard Lokta - Volterra omnivory model which will be the basis for our computations. In this model the predator population is divided into two stage classes, the juvenile predator and the adult predator. For our mathematical purposes, we will say this model of omnivory is a model consisting of one adult predator [P_2], one juvenile predator [P_1], one consumer [C], and one resource [R]. We consider a non-linear response omnivory model with top predator stage structure. We model the natural system with a system of ordinary differential equations.

$$\frac{dP_2}{dt} = \mu_P P_1 - m_P P_2 \tag{1}$$

$$\frac{dP_1}{dt} = \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}P_2 - (\mu_P + m_P)P_1 \tag{2}$$

$$\frac{dC}{dt} = C\left[\frac{e_{RC}\lambda_{RC}R}{1+\lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C} - m_C\right] \tag{3}$$

$$\frac{dR}{dt} = R\left[r\left(1-\frac{R}{K}\right) - \frac{\lambda_{RC}C}{1+\lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}P_1}{1+\lambda_{RP}h_{RP}R} - \frac{\lambda_{RP}P_2}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}\right] \tag{4}$$

with initial conditions

$$P_2(0) = c_1 > 0, \qquad P_1(0) = c_2 > 0, \qquad C(0) = c_3 > 0, \qquad and \qquad R(0) = c_4 > 0.$$

This forms an initial value problem

$$\frac{d\mathbf{x}}{dt} = \mathbf{f}(x), \qquad \mathbf{x}(0) = \mathbf{c} \tag{5}$$

on $D = \mathbb{R}_+ \times \mathbb{R}_+^4$ with the understood definitions for $\mathbf{f}$, $\mathbf{x}$, and $\mathbf{c}$.

Parameter r is the resource intrinsic rate of increase, K is the environmental carrying capacity of the resource, λ_{ij} is the search rate of species j for species i, h_{ij} is the time spent by species j handling species i, e_{ij} is the conversion efficiency of species i is converted to new offspring of species j, m_P and m_C are the natural mortality rates for both predator classes and consumers, and μ_P is the predator maturation rate. A summary of the variables and parameters is given in Table 1.

Table 1: Definitions of Variables and Parameters

Parameter	Definition
R	Resource density
C	Consumer density
P_1	Young/Small Predator density
P_2	Mature/Large Predator density
r	Resource intrinsic rate of increase
K	Environmental carrying capacity of the resource
λ_{RC}	Search rate of consumers for resources
λ_{RP}	Search rate of predators for resources
λ_{CP}	Search rate of predators for consumers
h_{RC}	Time spent by consumers handling resources
h_{RP}	Time spent by predators handling resources
h_{CP}	Time spent by predators handling consumers
e_{RC}	Conversion efficiency of resources into consumers
e_{RP}	Conversion efficiency of resources into predators
e_{CP}	Conversion efficiency of consumers into predators
m_C	Natural mortality rate of consumers
m_P	Natural mortality rate for both predator classes
μ_P	Predator maturation rate

4 Solution to System

The investigation of the long-term survival of species requires that a unique solution exists for all of time, $t \geq 0$. Since $\mathbf{f}$ and its partial derivatives

$$\frac{\partial \mathbf{f}}{\partial P_2} = \begin{pmatrix} -m_P \\ \frac{e_{RP}\lambda_{RP}R+e_{CP}\lambda_{CP}C}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C} \\ -\frac{\lambda_{CP}C}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C} \\ -\frac{\lambda_{RP}R}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C} \end{pmatrix}$$

$$\frac{\partial \mathbf{f}}{\partial P_1} = \begin{pmatrix} \mu_P \\ -(\mu_P + m_P) \\ 0 \\ -\frac{\lambda_{RP}R}{1+\lambda_{RP}h_{RP}R} \end{pmatrix}$$

$$\frac{\partial \mathbf{f}}{\partial C} = \begin{pmatrix} 0 \\ \frac{e_{CP}\lambda_{CP}P_2(1+\lambda_{RP}h_{RP}R)-e_{RP}\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2} \\ \frac{e_{RC}\lambda_{RC}R}{1+\lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2(1+\lambda_{RP}h_{RP}R)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2} - m_C \\ -\frac{\lambda_{RC}R}{1+\lambda_{RC}h_{RC}R} + \frac{\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2} \end{pmatrix}$$

$$\frac{\partial \mathbf{f}}{\partial R} = \begin{pmatrix} 0 \\ \frac{e_{RP}\lambda_{RP}P_2(1+\lambda_{CP}h_{CP}C)-e_{CP}\lambda_{RP}\lambda_{CP}h_{RP}CP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2} \\ \frac{e_{RC}\lambda_{RC}C}{(1+\lambda_{RC}h_{RC}R)^2} + \frac{\lambda_{CP}\lambda_{RP}h_{RP}CP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2} \\ r\left(1-\frac{2R}{K}\right) - \frac{\lambda_{RC}C}{(1+\lambda_{RC}h_{RC}R)^2} - \frac{\lambda_{RP}P_1}{(1+\lambda_{RP}h_{RP}R)^2} \\ -\frac{\lambda_{RP}P_2(1+\lambda_{CP}h_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2} \end{pmatrix}$$

are all continuous with respect to P_2, P_1, C, and R for all positive t. Our initial value problem (5) has one solution in D.

4.1 Existence and Uniqueness

We will now show a unique solution that can be extended to the left and right up to the boundary of D and exists for all $t \geq 0$ through a theorem.

Theorem 4.1. *The initial value problem (5) has a unique solution in* $\mathbb{R}_+^4$ *for all* $t \geq 0$.

Proof. As denoted earlier, $P_2(t)$, $P_1(t)$, $C(t)$, $R(t) \geq 0$ for all $t \geq 0$. Then

$$\frac{dR(t)}{dt} = R(t)\left[r\left(1-\frac{R(t)}{K}\right) - \frac{\lambda_{RC}C(t)}{1+\lambda_{RC}h_{RC}R(t)} - \frac{\lambda_{RP}P_1(t)}{1+\lambda_{RP}h_{RP}R(t)} - \frac{\lambda_{RP}P_2(t)}{1+\lambda_{RP}h_{RP}R(t)+\lambda_{CP}h_{CP}C(t)}\right]. \quad (6)$$

So we have the differential inequality

$$\frac{dR(t)}{dt} \leq R(t)r\left(1-\frac{R(t)}{K}\right).$$

However, the initial value problem

$$\frac{du(t)}{dt} = u(t)r\left(1-\frac{u(t)}{K}\right), u(0) = u_0$$

has a unique solution

$$u(t) = \frac{K}{1+\left(\frac{K}{u_0}-1\right)e^{-rt}}$$

Then applying a theorem and a lemma from Hale, we have that $R(t) = u(t)$ for $0 \leq t \leq \propto$. If in addition, we let $K_{max} = max(u_0, K)$, then $u(t) \leq K_{max}$ and we have

$$R(t) \leq K_{max} \quad for \quad 0 \leq t \leq \propto . \tag{7}$$

Also,

$$\frac{dC(t)}{dt} = C(t)\left[\frac{e_{RC}\lambda_{RC}R(t)}{1+\lambda_{RC}h_{RC}R(t)} - \frac{\lambda_{CP}P_2(t)}{1+\lambda_{RP}h_{RP}R(t)+\lambda_{CP}h_{CP}C(t)} - m_C\right] \leq e_{RC}\lambda_{RC}C(t)R(t)$$

Since $R(t) \leq K_{max}$, we have that

$$\frac{dC(t)}{dt} \leq e_{RC}\lambda_{RC}C(t)K_{max}$$

for $0 \leq t \leq \propto$. If we define

$$\Gamma_1 = e_{RC}\lambda_{RC}K_{max}$$
$$\Gamma_2 = e_{RP}\lambda_{RP}K_{max}$$

then by another lemma from Hale

$$C(t) \leq C(0)e^{\Gamma_1(t-0)} = c_3e^{\Gamma_1 t}. \tag{8}$$

This exponential function does not reach infinity in finite time. Further,

$$\frac{dP_1(t)}{dt} \leq (e_{RP}\lambda_{RP}R(t) + e_{CP}\lambda_{CP}C(t))P_2(t)$$

$$\frac{dP_2(t)}{dt} \leq \mu_P P_1(t)$$

Since $R(t) \leq K_{max}$ and $C(t) \leq c_3e^{\Gamma_1 t}$, we have that

$$\frac{dP_1(t)}{dt} \leq (\Gamma_2 + e_{CP}\lambda_{CP}c_3e^{\Gamma_1 t})P_2(t)$$

$$\frac{dP_2(t)}{dt} \leq \mu_P P_1(t)$$

for $0 \leq t \leq \propto$. Define $\phi = e_{CP}\lambda_{CP}c_3$ and rewrite the inequalities in matrix form.

$$\frac{d}{dt}\begin{pmatrix}\frac{P_1(t)}{P_2(t)}\end{pmatrix} \leq \begin{bmatrix} 0 & \Gamma_2 + \phi e^{\Gamma_1 t} \\ \mu_P & 0 \end{bmatrix}\begin{bmatrix} P_1(t) \\ P_2(t)\end{bmatrix} \tag{9}$$

Since,

$$2\begin{bmatrix} P_1(t) \\ P_2(t)\end{bmatrix}\frac{d}{dt}\begin{bmatrix} P_1(t) \\ P_2(t)\end{bmatrix} = \frac{d}{dt}\left\|\begin{matrix} P_1(t) \\ P_2(t)\end{matrix}\right\|^2 \tag{10}$$

we can multiply both sides of (9) by 2 and the row vector $[P_1(t)P_2(t)]$ to get

$$\left\|\begin{matrix} P_1(t) \\ P_2(t)\end{matrix}\right\|^2 \leq \frac{d}{dt}2(\Gamma_2 + \phi e^{\Gamma_1 t})P_1(t)P_2(t)$$

$$\leq (\Gamma_2 + \phi e^{\Gamma_1 t})((P_1(t))^2 + (P_2(t))^2).$$

So we have

$$\frac{d}{dt}\left\|\begin{matrix}P_1(t)\\P_2(t)\end{matrix}\right\|^2 \le (\Gamma_2+\phi e^{\Gamma_1 t})\left\|\begin{matrix}P_1(t)\\P_2(t)\end{matrix}\right\|^2. \tag{11}$$

If we define

$$\Lambda=\frac{\phi}{\Gamma_1}$$

and apply the same lemma from Hale to the scalar equation (11) we have

$$\frac{d}{dt}\left\|\begin{matrix}P_1(t)\\P_2(t)\end{matrix}\right\|^2 \le ((c_2)^2+(c_1)^2)e^{\Gamma t+\Lambda(e^{\Gamma t}-1)} \tag{12}$$

and this exponential function does not reach infinity in finite time. The above inequality ensures that $P_1(t)$ and $P_2(t)$ do not reach infinity in finite time. Therefore by a previous lemma and inequalities (7), (8), and (12) a unique solution for the initial value problem (5) exists for all $t \ge 0$. This completes the proof. □

5 Sensitivity Analysis

The first step in our sensitivity analysis method is to differentiate each right hand side of our model with respect to each of the model parameters. The partial derivatives of the right hand sides of the stage structure non-linear response omnivory model with respect to each model parameter is given in Table 2. Notice that each partial derivative is continuous with respect to t, P_2, P_1, C, and R for all positive parameter values.

Table 2: Partial Derivatives

Parameter	Partial of f_1	Partial of f_2
e_{RP}	0	$\frac{\lambda_{RP} RP_2}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}$
e_{CP}	0	$\frac{\lambda_{CP} CP_2}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}$
e_{RC}	0	0
λ_{RP}	0	$\frac{e_{RP}RP_2(1+\lambda_{CP}h_{CP}C)-e_{CP}\lambda_{CP}h_{RP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
λ_{CP}	0	$\frac{e_{CP}CP_2(1+\lambda_{RP}h_{RP}R)-e_{RP}\lambda_{RP}h_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
λ_{RC}	0	0
h_{RP}	0	-$\frac{\lambda_{RP}RP_2(e_{RP}\lambda_{RP}R+e_{CP}\lambda_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
h_{CP}	0	-$\frac{(\lambda_{CP})CP_2(e_{RP}\lambda_{RP}R+e_{CP}\lambda_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
h_{RC}	0	0
m_P	$-P_2$	$-P_1$
m_C	0	0
μ_P	P_1	$-P_1$
r	0	0
K	0	0

Parameter	Partial of f_3	Partial of f_4
e_{RP}	0	0
e_{CP}	0	0
e_{RC}	$\frac{\lambda_{RC}RC}{1+\lambda_{RC}h_{RC}R}$	0
λ_{RP}	$\frac{\lambda_{CP}h_{RP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$-\frac{RP_1}{(1+\lambda_{RP}h_{RP}R)^2}-\frac{RP_2(1+\lambda_{CP}h_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
λ_{CP}	-$\frac{CP_2(1+\lambda_{RP}h_{RP}R)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{\lambda_{RP}h_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
λ_{RC}	$\frac{e_{RC}RC}{(1+\lambda_{RC}h_{RC}R)^2}$	$-\frac{RC}{(1+\lambda_{RC}h_{RC}R)^2}$
h_{RP}	$\frac{\lambda_{RP}\lambda_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{(\lambda_{RP})^2R^2P_1}{(1+\lambda_{RP}h_{RP}R)^2}+\frac{(\lambda_{RP})^2R^2P_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
h_{CP}	$\frac{(\lambda_{CP})^2C^2P_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{\lambda_{RP}\lambda_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
h_{RC}	$-\frac{e_{RC}(\lambda_{RC})^2R^2C}{(1+\lambda_{RC}h_{RC}R)^2}$	$\frac{(\lambda_{RC})^2R^2C}{(1+\lambda_{RC}h_{RC}R)^2}$
m_P	0	0
m_C	-C	0
μ_P	0	0
r	0	$R\left(1-\frac{R}{K}\right)$
K	0	$\frac{rR^2}{K^2}$

By the following two theorems by Rosenwasser, we can differentiate the solution for our model with respect to each model parameter.

Theorem 5.1. *Assume that for any* $\alpha \in D_\alpha, \mathbf{x} = \mathbf{f}(t, \mathbf{x}, \boldsymbol{\alpha})$ *satisfies conditions of existence and uniqueness of solutions and this solution can be continued for* $t \geq t_0$. *This yields the existence of an open set* D *in the* $(t, \mathbf{x}, \boldsymbol{\alpha})$*-space in which* $\mathbf{f}(t, \mathbf{x}, \boldsymbol{\alpha})$ *is continuous with respect to* t *and* $\mathbf{x}$ *for all* $\boldsymbol{\alpha} \in D_\alpha$. *Also assume that the partial derivatives*

$$\frac{\partial f_i}{\partial x_j}(t, \mathbf{x}, \boldsymbol{\alpha}), \qquad for \;\; i, j = 1, \ldots, n$$

are continuous with respect to t *and* $\mathbf{x}$ *for all* $\boldsymbol{\alpha} \in D_\alpha$. *Then the solution* $\mathbf{x}(t, \boldsymbol{\alpha})$ *satisfying*

$$x(t, \boldsymbol{\alpha_0}) = \mathbf{x_0}$$

is continuous with respect to $\boldsymbol{\alpha}$ *for all* $\boldsymbol{\alpha} \in D_\alpha$ *and* $t \geq t_0$.

Theorem 5.2. *Let the conditions of the previous theorem hold. If in addition, the right hand sides of*

$$\begin{array}{rcl} \frac{dx_1}{dt} & = & f_1(t, x_1, \ldots, x_n) \\ \vdots & & \vdots \\ \frac{dx_n}{dt} & = & f_n(t, x_1, \ldots, x_n). \end{array}$$

have continuous partial derivatives in D *with respect to* $x_1, \ldots, x_n, \alpha_1, \ldots, \alpha_m$*, then the solution*

$$\mathbf{x}(t, \boldsymbol{\alpha_0}) = \mathbf{x_0}$$

has continuous partial derivatives with respect to $\alpha_1, \ldots, \alpha_m$.

5.1 Sensitivity Equations

The second step is a derivation of the sensitivity equations. The idea is to differentiate each differential equation with respect to each parameter. We then interchange the order of differentiation, and derive a linear system of equations for the sensitivities that solves:

$$\frac{d}{dt} S_{x_j,\alpha_i} = \sum_{k=1}^{n} \left(\frac{\partial f_j}{\partial x_k} S_{x_j,\alpha_i} \right) + \frac{\partial f_j}{\partial \alpha_i}$$

with the notation

$$S_{x_j,\alpha_i}(t) = \frac{\partial x_j(t)}{\partial \alpha_i}$$

where x_j is the jth component of the state, $j = 1, 2, 3, 4$ and $i = 1, 2, \ldots, 14$. Notice that we must also differentiate the initial conditions with respect to each parameter. Hence, we have the initial conditions

$$S_{x_j,\alpha_i}(0) = 0, \qquad for\ each \qquad x_j, \alpha_i.$$

Then by a theorem of Rosenwasser gives the justification of these formal mathematical manipulations. Table 2 gives the partial derivatives of the right hand side of the stage structure omnivory model with respect to the model parameters. The dependence upon time is suppressed for these calculations.

We use the term general sensitivity equations of the model for the system of linear ordinary differential equations

$$\frac{d}{dt} S_{x_j,\alpha_i} = \sum_{k=1}^{n} \left(\frac{\partial f_j}{\partial x_k} S_{x_j,\alpha_i} \right)$$

since the terms $\frac{\partial f_j}{\partial x_k}$ remain the same for each parameter. However, we use the term particular part of the equations of the model for the terms

$$\frac{\partial f_j}{\partial \alpha_i}$$

since they change for each parameter. Due to the fact that there are fourteen systems of four variables for the stage structure model that must be solved, we do not list all of these systems. However, we will list the general sensitivity equation for our model. Then the sensitivity equations are formed by adding the particular part of the equations. The particular part of the equations can be found on each row in Table 2. We will suppress the dependence upon time for the following model. The general sensitivity equations for the stage structure omnivory model are

$$
\begin{aligned}
\frac{d}{dt}(S_{P_2}) &= (-m_P)S_{P_2} + (\mu_P)S_{P_1} \\
\frac{d}{dt}(S_{P_1}) &= \left(\frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}\right)S_{P_2} - (\mu_P + m_P)S_{P_1} \\
&+ \left(\frac{e_{CP}\lambda_{CP}P_2(1+\lambda_{RP}h_{RP}R) - e_{RP}\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}\right)S_C \\
&+ \left(\frac{e_{RP}\lambda_{RP}P_2(1+\lambda_{CP}h_{CP}C) - e_{CP}\lambda_{RP}\lambda_{CP}h_{RP}CP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}\right)S_R \\
\frac{d}{dt}(S_C) &= \left(-\frac{\lambda_{CP}C}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}\right)S_{P_2} \\
&+ \left(\frac{e_{RC}\lambda_{RC}R}{1+\lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2(1+\lambda_{RP}h_{RP}R)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2} - m_C\right)S_C \\
&+ \left(\frac{e_{RC}\lambda_{RC}C}{(1+\lambda_{RC}h_{RC}R)^2} + \frac{\lambda_{CP}\lambda_{RP}h_{RP}CP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}\right)S_R \\
\frac{d}{dt}(S_R) &= \left(-\frac{\lambda_{RP}R}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}\right)S_{P_2} \\
&+ \left(-\frac{\lambda_{RP}R}{1+\lambda_{RP}h_{RP}R}\right)S_{P_1} \\
&+ \left(-\frac{\lambda_{RC}R}{1+\lambda_{RC}h_{RC}R} + \frac{\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}\right)S_C \\
&+ \left(r\left(1-\frac{2R}{K}\right) - \frac{\lambda_{RC}C}{(1+\lambda_{RC}h_{RC}R)^2} - \frac{\lambda_{RP}P_1}{(1+\lambda_{RP}h_{RP}R)^2}\right) \\
&- \left(\frac{\lambda_{RP}P_2(1+\lambda_{CP}h_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}\right)S_R
\end{aligned}
$$

with initial conditions

$$S_{P_2}(0) = 0, S_{P_1}(0) = 0, S_C(0) = 0, \text{ and } R(0) = 0$$

where we define

$$
\begin{aligned}
S_{P_2}(t) &= \frac{\partial}{\partial_{\alpha_i}} P_2(t), \\
S_{P_1}(t) &= \frac{\partial}{\partial_{\alpha_i}} P_1(t), \\
S_C(t) &= \frac{\partial}{\partial_{\alpha_i}} C(t), \\
S_R(t) &= \frac{\partial}{\partial_{\alpha_i}} R(t),
\end{aligned}
$$

We feel it is necessary to point out some of the difficulties that arise when using sensitivity equations methods. First, for each parameter that the original systems have, we must solve a system of linear differential equations. The number of differential equations in the state system dictates how many differential equations there will be in the linear sensitivity system. For our model, we have fourteen parameters and four variables. Therefore, for each parameter we must solve a first order linear system of four variables. Second, although the sensitivity equations are linear, they are "forced" by the solution to the state equations. However, the state equations are not dependent upon the sensitivities. Thus, we can form the couple system of states and sensitivities for the stage structure model

$$\frac{d\mathbf{y}}{dt}(t) = \mathbf{g}(t)$$

with initial condition

$$\mathbf{y}(0) = \mathbf{k}$$

where

$$\frac{d\mathbf{y}}{dt}(t) = \begin{pmatrix} \frac{dx_1}{dt}(t) \\ \vdots \\ \frac{dx_4}{dt}(t) \\ \frac{dS_{x_1}}{dt} \\ \vdots \\ \frac{dS_{x_4}}{dt} \end{pmatrix}, k = \begin{pmatrix} c_1 \\ c_2 \\ c_3 \\ c_4 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

and $\mathbf{g}(t)$ is the vector of right hand sides. Finally, a set of parameter values that seem appropriate for the natural system must be used in solving the sensitivity equations. The set of values for our parameters that we will use for our model are listed in Table 3.

Table 3: Values of Parameters

Parameter	Value
r	0.3
K	4
λ_{RC}	0.037
λ_{RP}	0.025
λ_{CP}	0.025
h_{RC}	3
h_{RP}	4
h_{CP}	4
e_{RC}	0.6
e_{RP}	0.36
e_{CP}	0.6
m_C	0.03
m_P	0.0275
μ_P	0.1

5.2 Sensitivities

We integrate the coupled systems using Matlab's fourth- and fifth-order adaptive step size algorithm known as ode45 to solve for the state variables and sensitivities. We use $1x10^-3$ for relative error tolerance and $1x10^-6$ for absolute error tolerance. For our calculations we use the initial conditions $(c) = (1, 1, 2, 3)^T$ for our stage structure omnivory model. Now, we must consider how to measure our sensitivities. We will use a weighted norm to measure of how small changes in the parameters affect the state variables. We use a weighted euclidean norm in four dimensions:

$$||S_{\alpha_i}||(t) = ||(S_{P_2}, \alpha_i, S_{P_1}, \alpha_i, S_C, \alpha_i, S_R, \alpha_i)^T||(t)$$
$$= \sqrt{w_1(S_{P_2}, \alpha_i)^2 + w_2(S_{P_1}, \alpha_i)^2 + w_3(S_C, \alpha_i)^2 + w_4(S_R, \alpha_i)^2}$$

The weights may be used to demonstrate that one species is more important in your measure. For our computations, we weight each species equally with a value of one. Notice, that we have a performance measure that is a function of the parameter and time only. The following are graphs of the norms of the sensitivities over time. We have defined three classes for the sensitivities based upon the numerical values over time: smaller, medium, and larger. See attached figures 1, 2, 3, and 4.

5.3 Results

As seen in the previous graphs, the largest value for the norm of the sensitivities for any parameter in our model is less than 410. In fact, the most sensitive parameter in our model is the predator mortality rate, m_P. This means that small changes in the predator mortality rate cause the largest change in the solution. Therefore, biologist should take careful measures in the field to accurately collect data for the predator mortality rate.

The next most sensitive parameters are the search and consumer mortality rates. All three of the search rates are more sensitive than the consumer mortality rate for the stage structure model. The maturation rate, μ_P, is more sensitive than the conversion efficiencies. The least sensitive parameter out of the conversion efficiencies and resource enrichment parameters, r and K is the carrying capacity, K.

The least sensitive parameters for our model is the handling times. Therefore, biologist need not be as accurate in collecting data for these parameters since they affect the solution the least. Of the handling times, the most sensitive parameter is h_{RP} and the least sensitive is h_{CP}.

6 Conculsions

There were three main ideas studied in this work. One was the formulation of a standard Lotka - Volterra stage structure omnivory model of increasing complexity. The second was the analysis of the parameter conditions under which our model ensured the coexistence of species. We used our model as an approximation to a natural system. We also showed that this system has a unique solution for all non-negative time. Finally, we used sensitivity analysis to analyze our model and provide information on meaningful parameter data collection.

From our results section the predator mortality rate needs the most accurate reading, while the resource carry capacity needs the least attention is the handling times need the least attention from biologists. From a biological point of view, our mathematical computations provide biologist with valuable information about how much effort should be put into obtaining parameter data in the field, as well as which parameter values affect the community the most.

Recall, that our system only used fourteen parameter values. Therefore it may be beneficial to use a model with more parameter values. This would all more parameter values to be evaluated, thus giving biologists a better idea of which field approximations need to be the most accurate. For future studies, it would be useful to investigate more complicated models and provide evidence to biologists which parameters are most sensitive and of utmost importance to each species survival.

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